Reproduction constrains the use of daily torpor by free-ranging common poorwills
(Phalaenoptilus nuttallii) (Aves: Caprimulgidae)

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(With 2 figures in the text)

The purpose of this study was to determine if common poorwills (Phalaenoptilus nuttallii) resist entering torpor during the breeding season. During the summers of 1991 and 1992, we studied poorwills in the Cypress Hills, Saskatchewan, Canada, near the northern limit of their distribution. Since poorwills are monogamous and share incubating and brooding responsibilities, we predicted that the non-incubating or non-brooding bird would enter torpor when stressed energetically (e.g. on cold and/or wet nights). Individuals carrying temperature-sensitive radio transmitters entered torpor significantly less often during the breeding season (two of 195 bird nights) than the non-breeding season (27 of 44 bird nights). During the breeding season we found no birds involved in an active nesting attempt in torpor. We conclude that reproduction constrains the use of torpor by adult birds, but why non-incubating and non-breeding birds did not enter remains unclear.

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Introduction

Temperate zone endotherms may periodically face energetic constraints due to extreme climatic conditions and ephemeral food supplies. Cold and wet conditions increase energy demands and may at the same time reduce food availability, particularly for insectivores (e.g. Racey, Speakman & Swift, 1987; Speakman & Racey, 1989). One means by which some mammals and birds cope with these constraints is through the use of torpor, which is characterized by a facultative and reversible reduction of metabolic rate and body temperature (Tb).

Laboratory studies of daily torpor (henceforth torpor) in hummingbirds (Trochilidae: Kruger, Prinzinger & Schumann, 1982) and goatsuckers (Caprimulgidae: Bartholomew, Howell & Cade, 1957) indicate that one or a combination of food shortage, reduced energy reserves, and cold or drought, can induce torpor. Under natural conditions, incubating or brooding hummingbirds...
TABLE I

Mean minimum monthly temperature and monthly precipitation in the Okanagan Valley (30 year means from Environment Canada, Penticton Airport, 344 m asl) of British Columbia and the Cypress Hills (30 year means from Environmental Canada, Cypress Hills Park, 1372 m asl) of Saskatchewan

<table>
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<tr>
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<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
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<tr>
<td>Temperature (°C)</td>
<td></td>
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<td></td>
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<tr>
<td>Okanagan Valley</td>
<td>6.1</td>
<td>9.8</td>
<td>12.0</td>
<td>11.6</td>
</tr>
<tr>
<td>Cypress Hills</td>
<td>3.4</td>
<td>7.2</td>
<td>11.0</td>
<td>10.3</td>
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<tr>
<td>Precipitation (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Okanagan Valley</td>
<td>29.1</td>
<td>27.6</td>
<td>21.1</td>
<td>26.5</td>
</tr>
<tr>
<td>Cypress Hills</td>
<td>63.1</td>
<td>85.1</td>
<td>41.3</td>
<td>49.1</td>
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(Calder & Booser, 1973) resist entering torpor except under extreme conditions, presumably because embryonic development is slowed and there is an increased risk of death for the embryo (Webb, 1987).

Brigham (1992) showed that free-ranging male and female common poorwills (Caprimulgidae: Phalaenoptilus nuttallii) in the south Okanagan Valley of British Columbia used torpor regularly outside the breeding season. More recent data (Kissner & Brigham, 1993), however, indicate that incubating and brooding poorwills can use torpor, but do so only under extreme conditions. The breeding range of poorwills extends into southwestern Saskatchewan (Csada & Brigham, 1992), an area that is cooler and wetter than the Okanagan Valley (Table I). These cooler and wetter conditions should place an additional energy demand on reproductively active individuals and thus may regularly force birds to use torpor during the breeding season.

The purpose of this study was to determine if poorwills use torpor during the breeding season. Since poorwills appear to be monogamous, with males and females sharing incubating and brooding responsibilities (Aldrich, 1935; Orr, 1948; Csada & Brigham, In press), we predicted that non-incubating or non-brooding individuals would enter torpor on climatically unfavourable (cold and/or wet) nights, while the incubating and brooding birds would not.

Poorwills are insectivorous birds distributed throughout western North America (Csada & Brigham, 1992). They feed at dusk, dawn, and periods of the night when the moon provides illumination (Brigham & Barclay, 1992). In the Okanagan Valley, poorwills make two breeding attempts (each clutch with two eggs) (Brigham & Barclay, 1992). If a clutch is lost or abandoned, replacement eggs are laid (Csada & Brigham, In press).

Materials and methods

The study was conducted from May to September in 1991 and 1992 in the West Block of Cypress Hills Provincial Park (49° 34' N, 109° 35' W) in Saskatchewan, Canada. The vegetation pattern of the West Block consists of open hill-sides intermixed with stands of lodgepole pine (Pinus contorta), white spruce (Picea glauca), and trembling aspen (Populus tremuloides; Kalcounis, Csada & Brigham, 1992a). Poorwill activity was centred over the open hill-sides and at forest edges.

Poorwills were captured by luring birds into mist nets using song playbacks (Brigham, 1992). We distinguished males from females by the presence and length of white tips on the rectrices (Chapman, 1925). Females have buff coloured rectrix tips about half the length of males.
Pre-calibrated, temperature-sensitive radio transmitters (model PD-2T, Holohil Systems Ltd., Woodlawn, Ontario, Canada) were affixed to 10 birds (1 nesting pair in 1991 and 3 nesting pairs and 2 reproductively active males in 1992) in a back-pack style arrangement using an elastic harness slipped over the wings (Brigham, 1992). The transmitters (2.4 g) represent approximately 5% of the bird's mass (47–49 g; Csada & Brigham, 1992). The effective range of signal reception varied from 1–4 km, depending upon terrain. The fact that radio-tagged birds bred successfully suggests that the transmitters did not negatively affect their behaviour.

The transmitters were affixed so that the temperature sensor was in contact with the interscapular skin of the back. We determined skin temperature (Tsk) by averaging 3 timings of the interval required for 10 transmitter pulses and then compared the average to calibration curves prepared for each transmitter. Tsk was measured at 20 min intervals from approximately midnight until activity ceased at dawn and opportunistically during the daytime. We estimated core (=cloacal) temperature (Tc) from Tc = 1.58 + 0.9598Tsk (Brigham, 1992). Because Tb of active poorwills varies from 35° to 44°C under laboratory conditions (Bartholomew, Hudson & Howell, 1962), we followed Hudson (1978) and defined torpor as Tc < 30°C. Below this temperature poorwills cannot respond immediately to external stimuli (Bartholomew et al., 1957).

We defined the breeding season as having started when we first found eggs and having ended when brooding ceased. In 1991, the first eggs were found on 5 July and brooding continued through 3 September, when the study ended. Therefore, the end of the breeding season was not observed. In 1992, the first eggs were found on 7 June and the last active nest was abandoned on 17 August. Incubating and brooding birds were considered to be reproductively active.

We measured minimum nightly temperatures (Tmin) on nights when birds were tracked using a maximum–minimum thermometer placed 1 m above the ground and within 1 km of the day roost or nest locations of birds carrying transmitters. The thermometer was usually within ±5 m (range 0–30 m) of radio-tagged birds in terms of vertical elevation.

To assess insect abundance, 2 cylindrical sticky traps (40 cm long and 10 cm in diameter), coated with axle grease (Kalcounis, Csada & Brigham, 1992b) and hung (20 cm apart) 1.5 m above the ground, and one combination light and suction trap (1992 only; Kunz, 1988) were set from sunrise to sunset in habitats similar to those where poorwills commonly foraged. Insects caught were identified to order and counted. Only moths, beetles and flies were considered in the analysis since these groups constitute >95% of the diet (Csada, Brigham & Pittendrigh, 1992; Bayne & Brigham, 1994).

In 1992, we defined cool nights as those with Tmin ≤ 6°C and warm nights as those with Tmin > 6°C (no birds entered torpor on warm nights). We measured insect abundance on 17 cool nights (we tracked birds on 11 of these) and 12 warm nights (birds were tracked on 7 of these). We radio-tracked birds on 19 cool nights during the breeding season and on 11 cool nights outside the breeding season. Insect abundance was measured on 6 of these nights during the breeding season and on 5 nights outside.

In 1991 and 1992, birds were tracked on 9 and 11 nights, respectively, during the period of 17 August–2 September. Insect abundance was measured (sticky traps only) on 3 of these nights in 1991 and on 5 of these nights in 1992.

We used a 2 × 2 contingency table (following a Yates continuity correction) to determine if poorwills used torpor differentially between the breeding and non-breeding seasons. Analysis of variance, after testing for homogeneity of variance and normality, was used for all 2-sample comparisons. Data are presented as means ±1 S.E. We used a rejection level of P < 0.05.

Results

Individuals entered torpor significantly less often (χ² = 117.0, P < 0.001) during the breeding season (two of 195 bird nights; Table II) than outside the breeding season (27 of 44 bird nights). Two birds tracked on the same night equals two bird nights. Each bird was tracked for an average
of 26.6 ± 4.8 nights (range 5–50). Neither member of the nesting pair used torpor in 1991 (all of the tracking period defined as in the breeding season), however, all but one female entered torpor at least once in 1992.

We found no poorwills of either sex in torpor while incubating eggs or brooding chicks. Both instances of birds entering torpor during the breeding season occurred on the night of 30 June 1992 and involved two males, which had abandoned their nests three and nine days previously. The 30th of June was the third consecutive cool night accompanied by heavy rain, which may have restricted or prevented foraging completely. We found no evidence that either male contributed to a subsequent nesting attempt.

In 1992, torpor was used regularly after 21 August, when all young had fledged. Outside the breeding season, the use of torpor did not vary substantially among individuals. On six of the eight nights when torpor was used and when we monitored 

Typically, birds became active at dusk and entered torpor near the end of nautical twilight (when the sun is > 12° below the horizon; Martin, 1990). This suggests that the birds may use cues available during the dusk foraging period to determine whether or not to enter torpor. However, on at least six nights, birds entered torpor prior to dusk and did not forage at all. It is likely that inclement weather also prevented other dusk foraging bouts. The length of torpor bouts appeared to be influenced by environmental conditions and bouts lasted at least 12 h (n = 8) with 

Insect abundance was significantly higher on warm nights than on cool nights for 1992 as a whole (suction traps: \( F = 8.68, P < 0.01 \); sticky traps: \( F = 11.37, P < 0.01 \); Fig. 1) and, when considered separately, on the subset of nights when we tracked birds (suction traps: \( F = 14.64, P < 0.05 \); sticky traps: \( F = 7.79, P < 0.05 \)). There was no significant difference in insect abundance (suction traps: \( F = 0.12, P > 0.50 \); sticky traps: \( F = 0.01, P > 0.50 \); Fig. 2) between cool nights inside versus outside the breeding season. During the breeding season, torpor was used on only one of 19 cool nights, however, outside the breeding season, torpor was used on eight of 11 cool nights.

### Table 1

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<thead>
<tr>
<th></th>
<th>One member of pair</th>
<th>Both members of pair</th>
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<td>NT</td>
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<tr>
<td><strong>Breeding Season</strong></td>
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<td>Eggs present</td>
<td>0</td>
<td>31</td>
</tr>
<tr>
<td>Chicks present</td>
<td>0</td>
<td>20</td>
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<tr>
<td>Eggs/chicks absent</td>
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<td>42</td>
</tr>
<tr>
<td><strong>Non-breeding Season</strong></td>
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<tr>
<td>Eggs/chicks absent</td>
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<td>0</td>
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</table>
USE OF TORPOR BY POORWILLS

For the period of 17 August–2 September in 1991 and 1992, there was no significant difference in the average $T_{\text{min}}$ (3.4 ± 2.9°C vs. 2.8 ± 1.6°C; $F = 0.07, P > 0.50$) or insect abundance (10.3 ± 2.0 vs. 9.0 ± 3.5; sticky traps: $F = 0.08, P > 0.50$). During this period in 1991, birds were reproductively active and torpor was not used ($n = 9$ nights), while in 1992, when no incubating or brooding took place, torpor was used on six of 11 nights.

**Discussion**

Our results indicate that, although inclement weather occurred regularly during both the breeding and non-breeding seasons, poorwills resisted entering torpor during the breeding
season. Outside the breeding season, however, torpor was used regularly with bouts lasting at least 12 hours and birds allowing $T_c$ to drop below 10 °C. We found that incubating or brooding birds did not enter torpor, but during the breeding season two birds that had recently abandoned their nests did enter torpor.

In 1992, there was no significant difference in insect availability between cool nights inside the breeding season and cool nights outside, yet torpor was used only when birds were not reproductively active. For the period of 17 August–2 September, there was no significant difference in the average $T_{\text{min}}$ or insect abundance between 1991 and 1992. Torpor was used only in 1992, however, when no reproductive activity was observed. These results strongly support the suggestion that reproduction constrains the use of torpor by adult birds.

Reproductively active adults may resist entering torpor as a means of balancing the costs of reproduction and survival. The costs of reproduction can be considered at two levels: 1) ecological costs to the parents, and 2) physiological costs to the eggs or chicks.

A potential ecological cost to the parents of using torpor during the breeding season is an increased risk of predation. Poorwills, though very cryptic when torpid, cannot respond behaviourally to an approaching predator (Bartholomew et al., 1957), thus they possess no means for active defence against predators if discovered. Since nest sites are found in places with less vegetative cover and physical protection than day roosts used outside the breeding season (RDC, pers. obs.), nest sites tend to be more conspicuous than day roosts. This might make torpid incubating or brooding adults more vulnerable to predation than torpid individuals outside the breeding season.

A potential physiological cost to the embryo or chick of incubating or brooding birds using torpor is delayed development or even death (Webb, 1987). The temperature range for optimum development of eggs (37 to 38 °C in domestic fowl) is considered to be narrow (Hafthorn, 1988). In addition, a 'physiological zero temperature' (PZT), below which no embryonic development at all takes place, exists and is approximately 25 to 27 °C (although this has not been measured precisely for poorwills; Hafthorn, 1988). If eggs are kept for long periods (e.g. several hours) at temperatures between the optimum and PZT, abnormal embryonic development may result (Hafthorn, 1988). Therefore, the use of torpor by incubating or brooding birds may result in the loss of the eggs.

Several studies (e.g. Vitale et al., 1985; Ruby et al., 1993) of small mammals suggest that the reduced use of torpor during the breeding season is due to high levels of reproductive hormones. For males, depressed body temperatures result in abnormal sperm production (Jagiello et al., 1992), which is hormonally controlled by testosterone. Poorwill nests suffer from a high rate of nest predation (Csada & Brigham, In press), therefore, non-incubating or non-brooding males may have to remain homeothermic to stay in reproductive condition. This elevated hormone level argument may not apply to temperate bats, which are ecologically similar to poorwills (e.g. Brigham & Fenton, 1991), since these bats are seasonal breeders.

Unfortunately, none of the above arguments can explain our observations of non-incubating and non-brooding birds not entering torpor. One could argue that the non-incubating or non-brooding birds should be more likely to use torpor than birds outside the breeding season, even if it increases their risk of predation, because they would have more to gain since there is a greater fitness loss if death occurs during the breeding season. Further, the fact that there was not a progressive shift to non-incubating or non-brooding males using torpor late in the breeding season, when the likelihood of laying a successful replacement clutch decreases, contradicts the elevated hormone argument. We are simply unsure as to why the non-incubating and non-brooding birds do not regularly enter torpor.
USE OF TORPOR BY POORWILLS

Energetically stressed incubating or brooding birds are physiologically capable of entering torpor (Kissner & Brigham, 1993), yet our results suggest it is not a common occurrence. We predict that torpor during the reproductive cycle will occur at the start of incubation, since younger embryos are more tolerant to prolonged cold periods (Tazawa & Rahn, 1986), or late in the brooding period when chicks may be capable of entering torpor themselves. If conditions persist in which nesting birds cannot maintain a positive energy balance, nest desertion is expected to occur.

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REFERENCES


